

# Burrowing Performance of Some Tropical Pacific Gastropods

by

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**Abstract.** The burrowing performance of 33 gastropod species from Guam, Mariana Islands, was assessed in a substrate of moderately coarse loose sand by calculating the burrowing rate index (BRI), defined as the cube root of the animal's mass in grams divided by the time in minutes necessary to achieve complete burial. Rapid burrowing (BRI 1.0 or higher) characterized only three species, and was associated with a large foot and a smooth shell. Despite the mechanical advantages of a wedge shape, species with a conical outline (as exemplified in the genus *Conus*) were slow burrowers (BRI 0.54 or less) and had a narrow aperture and a small foot. The slowest burrowers were high-spined or narrow-apertured species usually possessing spiral or axial sculpture on the shell's exterior.

With the possible exception of ratchet sculpture (ribs whose anterior flanks are less steep than the posterior flanks), no shell characteristic is diagnostic of rapid burrowing. Frequent convergence to the *Oliva* and *Conus* forms cannot be interpreted to imply functional convergence for rapid locomotion.

The burrowing performance of gastropods is comparable to that of pelecypods. We speculate that burrowing is generally ineffective as a method of escape from predators, but is instead effective in preventing detection by enemies.

## INTRODUCTION

ACTIVE BURROWING in unconsolidated sediments is a common mode of life in marine gastropods. Well over half the gastropod species in shallow-water assemblages from sand and mud habitats in the tropical Indo-west-Pacific region are burrowers belonging to many prosobranch and opisthobranch families. In contrast to crawling, which has been studied extensively (MILLER, 1974; LINSLEY, 1978; PALMER, 1980; KENT, 1983; DIMMOCK, 1985), burrowing in gastropods has received comparatively little attention. Of the available studies, those of SIGNOR (1982a, b, 1983) are unique in that they provide comparative data on burrowing performance and on the way in which shell shape influences burrowing ability. His work deals only with high-spined species, however, and no large-scale survey of burrowing in gastropods comparable to STANLEY's (1970) study of pelecypods has been undertaken to date.

In this paper we present data on the burrowing performance of 33 shallow-water gastropods from sandy habitats in Guam, the southernmost of the Mariana Islands in the tropical western Pacific. We undertook this survey with three questions in mind. First, how much can be inferred about burrowing in fossil gastropods from a knowledge of the relationship between shell form and bur-

rowing in a geometrically diverse array of living species? In particular, can the frequent convergence to the *Conus* and *Oliva* forms be attributed to selection for high burrowing performance? Second, how does the performance of gastropods compare with that of other burrowing invertebrates, notably the well-studied pelecypods? Finally, how effective is burrowing as a method of escape from predators?

Burrowing performance may be enhanced by several features of the gastropod shell. Rapid burrowing may be achieved either by reducing drag or by increasing power, or both. Drag is minimized by a streamlined shell, characterized by a wedgelike anterior end, a smooth exterior, and a gently curving or straight lateral profile. This morphology promotes the movement of sedimentary particles backward along the shell surface and prevents particles from being carried along by the moving animal. In order to prevent back slippage during burrowing, some burrowers have evolved cuesta or ratchet sculpture in which the anterior flanks of exterior ridges are less steep than the posterior flanks (STANLEY, 1969, 1970; SCHMALFUSS, 1978; SAVAZZI, 1981, 1982; SIGNOR, 1982a, b, 1983). Power in gastropods is provided by the foot. A large foot, associated with a broad aperture or the internalization of the shell,

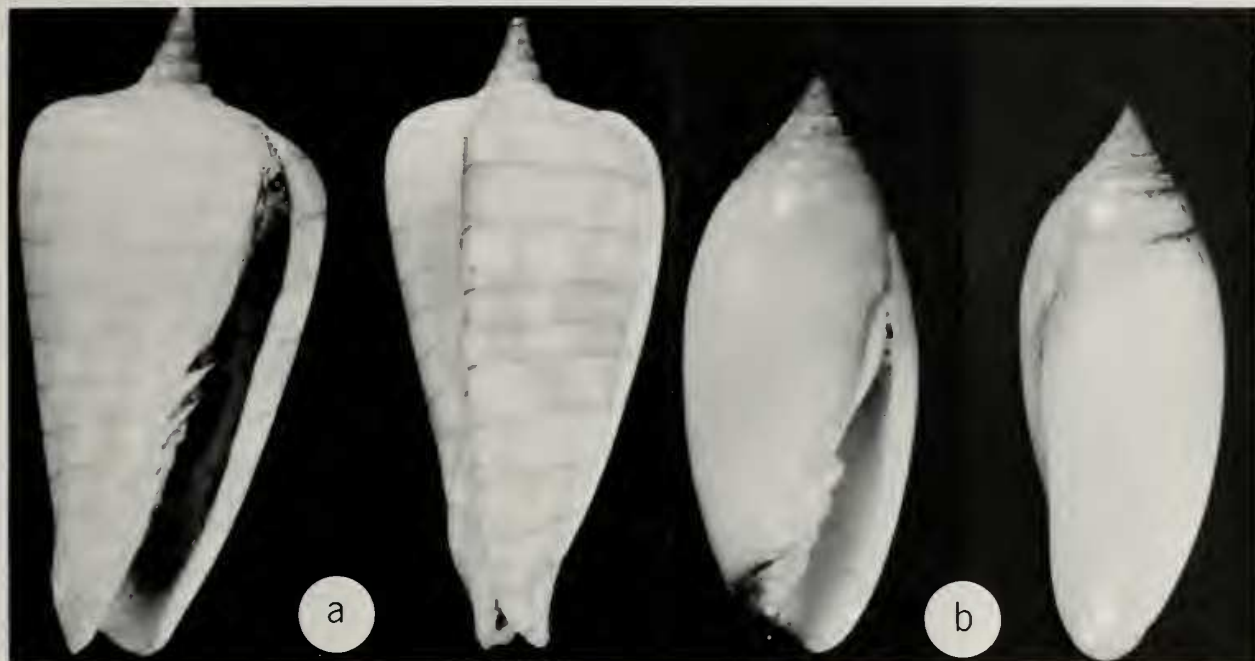


Figure 1

Shells of two species of *Imbricaria*. a. A specimen of *I. conularis*, 15.8 mm long, viewed from the aperture (left) and laterally (right). b. A specimen of *I. olivaeformis*, 12.7 mm long, viewed from the aperture (left) and laterally (right). Photographs and plate composition by Roy Kropp.

should therefore characterize rapid burrowers (SIGNOR, 1982a, b, 1983). In short, the highest rates of burrowing should be associated with conical, smooth, ratcheted, or large-apertured shells.

#### MATERIALS AND METHODS

Gastropods of 33 species were collected during July and August, 1984, in sandy habitats at five sites in Guam, ranging from the intertidal zone to a depth of 12 m. They were maintained at the University of Guam Marine Laboratory in running seawater in aquaria and allowed to bury in sand for periods not exceeding three days before burrowing performance was measured.

All burrowing trials were staged at ambient seawater temperature (ca. 28°C) in a small aquarium filled with medium to coarse calcareous sand from the reef flat at Pago Bay in front of the laboratory (gravel-pebble fraction 3%, coarse-sand fraction 46%, medium-sand fraction 46%, fine-sand fraction 5%, by weight). At the beginning of a trial, the snail was placed on the surface of the sand. Burrowing time in minutes was measured from the onset of burrowing movements until the snail had buried itself completely. Most individuals were used only once, but a few were allowed to bury several times in succession. Following the trial, we measured animal mass (wet weight in grams) and four linear shell dimensions in millimeters:

shell length (distance from apex to anterior end), maximum shell width (taken to be perpendicular to length), aperture length (distance from anterior to posterior end of aperture), and aperture width (greatest distance from outer lip to left edge of smooth parietal area). Apertural dimensions were not measured in olivids because the left margin of the aperture is not well demarcated in these animals, in which the foot extends over the shell's exterior.

In order to compare burrowing performances among animals of different shapes and sizes, STANLEY (1970) devised the burrowing rate index (BRI), which he defined as the cube root of mass in grams divided by the time in minutes required for complete burial. SIGNOR (1982a) modified the index by replacing mass with volume in the numerator, because he believed that volume was more accurately measured. We chose to use Stanley's index not only because our data would then be directly comparable to his, but also because wet weight was quickly and accurately measured. Moreover, our results on terebrids closely parallel Signor's, so that we are confident that the patterns in our data are not artifacts of the particular index we used.

We tested the size-independence of the burrowing rate index in *Conus pulicarius*, the species for which the largest number and greatest size range of individuals were available. The least-squares fit of the data conforms to the equation

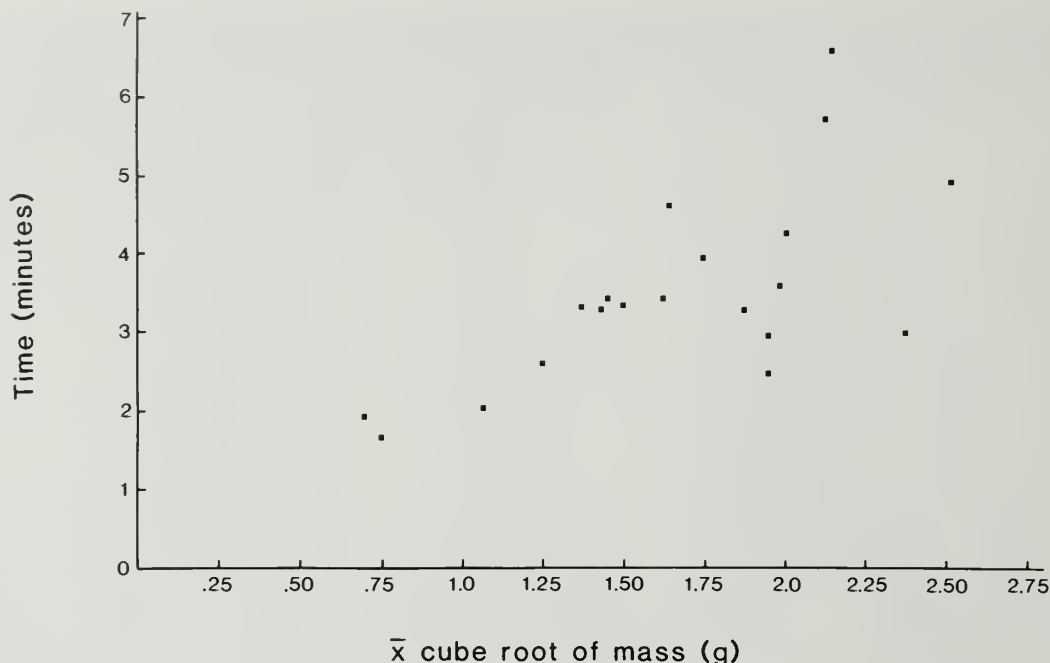


Figure 2

Plot of burrowing time (minutes) against cube root of mass (wet weight) for *Conus pulicarius*. As expected, the data reveal a straight-line relationship over most of the range in mass. Only the very large animals show a conspicuous scatter of points. Some of these large animals may remain partly exposed in the field, for the upper surface of the shell in these individuals may become pitted.

$$Y = 1.697X + 0.681 \quad (r^2 = +0.42, n = 20, P < 0.01),$$

where Y is burrowing time in minutes and X is the cube root of mass in grams (Figure 2). Almost all of the scatter of points was confined to large animals (mass 8 g and greater).

## RESULTS

We investigated interspecific patterns of shell form and burrowing performance by analyzing the data in Table 1. The data are pictorially summarized in Figure 3. As expected, the 13 smooth-shelled species burrowed relatively faster than did the 20 spirally or axially sculptured species ( $P < 0.01$  for both mean and maximum BRI, Mann-Whitney U-Test). Among high-spined species (ratio of aperture length to shell length less than 0.5), the three species with predominantly spiral sculpture all had a lower BRI than did the four with predominantly axial sculpture. No difference in burrowing performance was observed between the five spirally and six axially sculptured species in the low-spined group.

Species with a large foot were the fastest burrowers in both absolute and relative terms. The three fastest species (*Oliva miniacea*, *O. annulata*, and *Natica gualteriana*) are smooth-shelled, whereas the fourth fastest (*Nassarius*

*granifer*) has a pustulose sculpture. In *Oliva*, the foot extends over the outer shell surface during burrowing, so that rapid speed is achieved despite the narrowly elongate shell opening.

The slowest burrowers were either very high-spined (*Terebra funiculata*, *T. babylonia*, *Cerithium nesioticum*, *Otopleura nodicincta*) or narrow-apertured (*Conus tessulatus*, *Subcancilla verrucosa*), and all had a small shell opening. There was a highly significant correlation between relative aperture length (aperture length to shell length ratio) and BRI (Spearman Rank Correlation, +0.43 for mean BRI, +0.46 for maximum BRI;  $P < 0.01$ ); that is, low-spined species are generally faster burrowers than are high-spined forms.

Species with a conical outline (*Imbricaria conularis*, *I. punctata*, and species of *Conus*) varied widely in burrowing performance, but none was fast. Among narrow-apertured species, there was not even a hint of a difference in burrowing performance between the eight conical species and the 10 species with a more cylindrical outline (*Vexillum*, *Oliva*, *Subcancilla*, *Graphicomassa*, and *Imbricaria olivaeformis*).

Within species, there was considerable variation in shell shape (shell length to shell width ratio) and in aperture shape (Table 1). We found no correlations between bur-

Table 1

Burrowing performance and shell form in gastropods from Guam. *Key:* Sc: sculpture—ax, axial; ra, ratcheted; sm, smooth; sp, spiral; tu, tuberculate. n: number of individuals tested. Sh.Sh.: shell shape—ratio of shell length to shell width. RAL: relative aperture length—ratio of aperture length to shell length. Ap.Sh.: aperture shape—ratio of aperture length to aperture width. Data are given with standard deviation whenever n is 4 or greater.

| Species   | Sc | n  | Sh.Sh.      | RAL         | Ap.Sh.      | Burrowing rate index |      |
|---|----|----|-------------|-------------|-------------|----------------------|------|
|   |    |    |             |             |             | Mean                 | Max. |
| Family CERITHIIDAE                                  |    |    |             |             |             |                      |      |
| <i>Cerithium nesioticum</i> Pilsbry & Vanatta, 1905 | sp | 1  | 2.86        | 0.26        | 1.73        | 0.17                 | 0.17 |
| <i>Rhinoclavis aspera</i> (Linnaeus, 1758)          | ra | 2  | 2.96        | 0.36        | 1.44        | 0.32                 | 0.36 |
| <i>R. articulata</i> (Adams & Reeve, 1850)          | ra | 1  | 2.88        | 0.33        | 1.09        | 0.25                 | 0.25 |
| <i>R. fasciata</i> (Bruguière, 1792)                | ra | 4  | 4.62 ± 0.08 | 0.27 ± 0.01 | 1.42 ± 0.08 | 0.32 ± 0.12          | 0.44 |
| Family NATICIDAE                                    |    |    |             |             |             |                      |      |
| <i>Natica gualteriana</i> (Récluz, 1844)            | sm | 1  | 1.38        | 0.72        | 1.22        | 1.38                 | 1.38 |
| Family COLUMBELLIDAE                                |    |    |             |             |             |                      |      |
| <i>Graphicomassa ligula</i> (Duclos, 1840)          | sm | 1  | 2.61        | 0.56        | 3.83        | 0.33                 | 0.33 |
| Family NASSARIIDAE                                  |    |    |             |             |             |                      |      |
| <i>Nassarius granifer</i> (Kiener, 1834)            | tu | 3  | 1.56        | 0.90        | 1.38        | 0.83                 | 1.03 |
| Family COSTELLARIIDAE                               |    |    |             |             |             |                      |      |
| <i>Vexillum cadaverosum</i> (Reeve, 1844)           | ax | 3  | 2.12        | 0.56        | 4.02        | 0.18                 | 0.25 |
| <i>V. exasperatum</i> (Gmelin, 1791)                | ax | 11 | 2.48 ± 0.21 | 0.56 ± 0.03 | 3.65 ± 0.37 | 0.44 ± 0.10          | 0.61 |
| <i>V. michaudi</i> (Crosse & Fischer, 1864)         | ax | 6  | 3.03 ± 0.24 | 0.55 ± 0.02 | 5.03 ± 0.33 | 0.24 ± 0.03          | 0.27 |
| <i>V. semifasciatum</i> (Lamarck, 1811)             | ax | 2  | 2.39        | 0.58        | 3.94        | 0.25                 | 0.38 |
| Family OLIVIDAE                                     |    |    |             |             |             |                      |      |
| <i>Oliva miniacea</i> Röding, 1798                  | sm | 3  | 2.13        | —           | —           | 3.15                 | 3.55 |
| <i>O. annulata</i> Gmelin, 1791                     | sm | 3  | 2.10        | —           | —           | 2.72                 | 3.16 |
| Family MITRIDAE                                     |    |    |             |             |             |                      |      |
| <i>Ziba fulgetrum</i> (Reeve, 1844)                 | sp | 1  | 2.71        | 0.68        | 5.75        | 0.45                 | 0.45 |
| <i>Subcancilla filaris</i> (Linnaeus, 1771)         | sp | 5  | 2.68 ± 0.40 | 0.60 ± 0.03 | 3.81 ± 0.40 | 0.37 ± 0.13          | 0.61 |
| <i>S. verrucosa</i> (Reeve, 1845)                   | sp | 1  | 2.88        | 0.58        | 5.00        | 0.37                 | 0.37 |
| <i>Imbricaria conularis</i> (Lamarck, 1811)         | sm | 7  | 2.26 ± 0.04 | 0.83 ± 0.02 | 6.22 ± 0.49 | 0.50 ± 0.10          | 0.65 |
| <i>I. olivaeformis</i> (Swainson, 1821)             | sm | 10 | 2.48 ± 0.19 | 0.79 ± 0.05 | 6.09 ± 0.39 | 0.31 ± 0.13          | 0.53 |
| <i>I. punctata</i> (Swainson, 1821)                 | sm | 2  | 1.88        | 0.92        | 5.18        | 0.33                 | 0.41 |
| Family CONIDAE                                      |    |    |             |             |             |                      |      |
| <i>Conus catus</i> Hwass, 1792                      | sp | 1  | 1.54        | 0.88        | 5.28        | 0.54                 | 0.54 |
| <i>C. coronatus</i> Gmelin, 1791                    | sm | 6  | 1.67 ± 0.07 | 0.88 ± 0.04 | 7.18 ± 0.61 | 0.27 ± 0.10          | 0.44 |
| <i>C. eburneus</i> Hwass, 1792                      | sm | 3  | 1.71        | 0.93        | 8.17        | 0.41                 | 0.47 |
| <i>C. pulicarius</i> Hwass, 1792                    | sm | 20 | 1.72 ± 0.08 | 0.92 ± 0.02 | 7.57 ± 0.55 | 0.49 ± 0.12          | 0.79 |
| <i>C. tessulatus</i> Born, 1778                     | sm | 1  | 2.05        | 0.86        | 8.15        | 0.11                 | 0.11 |
| Family TEREBRIDAE                                   |    |    |             |             |             |                      |      |
| <i>Hastula solida</i> (Deshayes, 1857)              | sm | 1  | 3.96        | 0.35        | 2.87        | 0.60                 | 0.60 |
| <i>Terebra affinis</i> Gray, 1834                   | ax | 8  | 4.05 ± 0.29 | 0.31 ± 0.03 | —           | 0.41 ± 0.09          | 0.60 |
| <i>T. babylonia</i> Lamarck, 1822                   | sp | 1  | 6.96        | 0.16        | 1.68        | 0.18                 | 0.18 |
| <i>T. felina</i> Dillwyn, 1817                      | sm | 1  | 4.24        | 0.27        | 1.40        | 0.26                 | 0.26 |
| <i>T. funiculata</i> Hinds, 1844                    | sp | 2  | 5.79        | 0.21        | 1.41        | 0.12                 | 0.13 |
| <i>T. maculata</i> (Linnaeus, 1758)                 | sm | 4  | 3.57 ± 0.26 | 0.38 ± 0.07 | —           | 0.51 ± 0.07          | 0.58 |
| Family TURRIDAE                                     |    |    |             |             |             |                      |      |
| <i>Eucithara stromboides</i> (Reeve, 1846)          | ax | 2  | 2.11        | 0.66        | 3.27        | 0.51                 | 0.59 |
| Family PYRAMIDELLIDAE                               |    |    |             |             |             |                      |      |
| <i>Otopleura nodicincta</i> (A. Adams, 1855)        | ax | 2  | 2.26        | 0.48        | 1.84        | 0.17                 | 0.19 |
| Family ACTEONIDAE                                   |    |    |             |             |             |                      |      |
| <i>Pupa nivea</i> (Angas, 1860)                     | sp | 3  | 2.16        | 0.74        | 2.87        | 0.23                 | 0.29 |



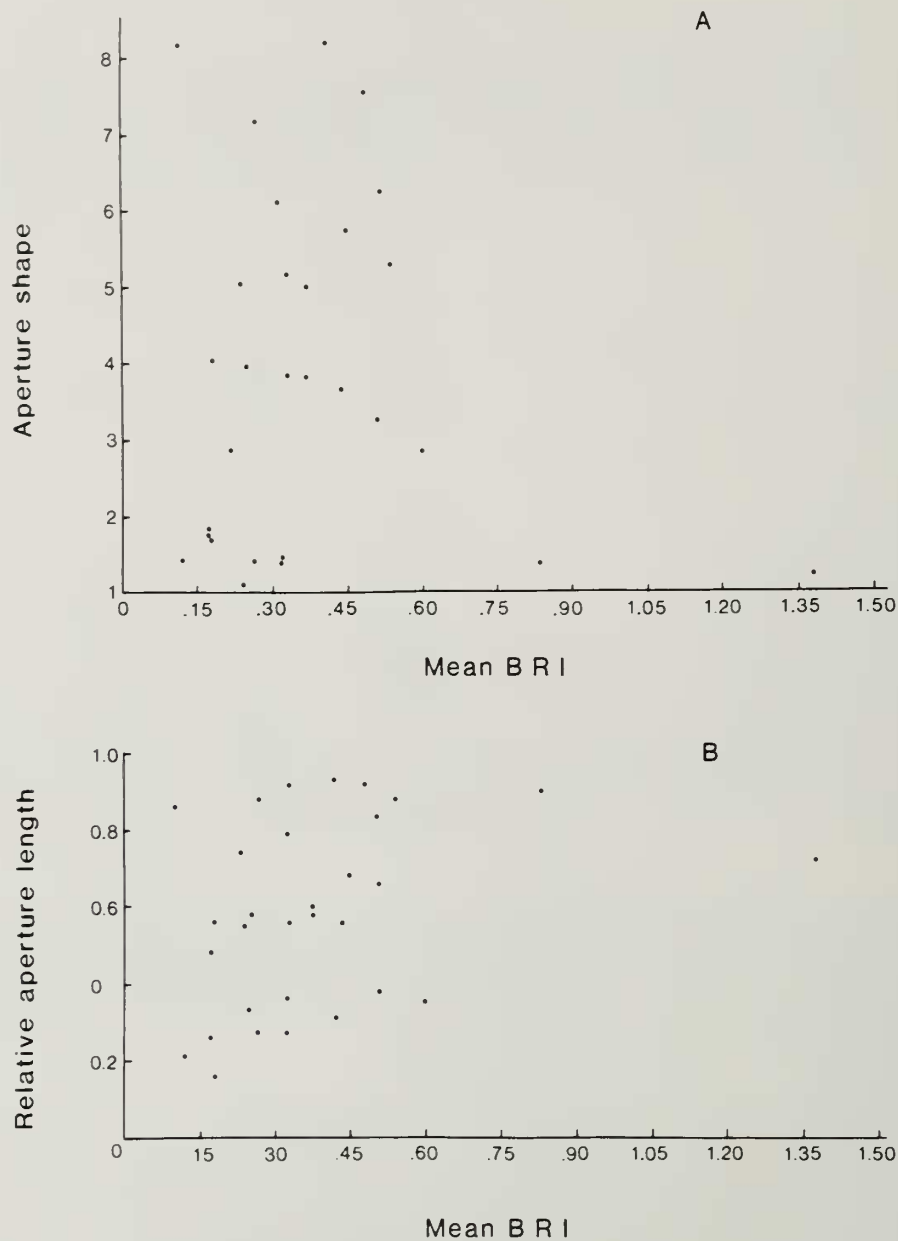


Figure 3

Plot of aperture shape (A) and relative aperture length (B) against mean burrowing rate index (BRI) for 33 species of gastropod. Aperture shape is defined as aperture length divided by aperture width. Relative apertural length is defined as aperture length divided by shell length. Data on which the figure is based are given in Table 1.

rowing performance and either shell shape or aperture shape in any of the species for which the number of individuals was eight or greater (*Vexillum exasperatum*, *Imbricaria olivaeformis*, *Conus pulicarius*, and *Terebra affinis*;  $P > 0.20$  in all cases).

## DISCUSSION

In his studies of burrowing in high-spired ("turritelliform") gastropods, SIGNOR (1982a, b, 1983) found that the burrowing rate index of terebrids with a squat shell

was higher than that in slender species. Our results corroborate his findings not only for terebrids, but for burrowing gastropods generally. Signor's suggestion that the faster burrowing results from greater power (that is, from the larger size of the foot) seems to be a reasonable explanation for this pattern.

Signor also found that strong sculpture was associated with a slender shape in terebrids, and that it generally implies a slow rate of burrowing. Again, our results are in accord with this finding. Among high-spined species, which drag the shell behind them as they burrow, axial sculpture oriented in the direction of movement is more conducive to burrowing than is spiral sculpture that is oriented at right angles to the direction of movement. The only form of sculpture that enhances burrowing is cuesta or ratchet sculpture, but even this feature is found only in relatively slowly burrowing gastropods such as species of *Rhinoclavis*, *Terebra*, and *Neocancilla*.

With the possible exception of ratchet sculpture, which among gastropods is found only in burrowers (SIGNOR, 1983), none of the shell features of rapidly burrowing gastropods is diagnostic of the burrowing habit. Cowries (family Cypraeidae), for example, have a large foot and a smooth, often highly streamlined shell, but they are incapable of burrowing. The conical shape is common among diverse burrowing gastropods (Marginellidae, Conidae, the cassid *Morum*, the mitrids *Imbricaria* and *Pterygia*, and most Conidae and some Turridae), but it also occurs widely among epifaunal crawlers (the strombid *Conomurex*, the columbellids *Parametaria* and *Minipyrone*, many species of Conidae, and the high intertidal pulmonate family Melampidae). It is possible that the conical form originated in burrowing forms and was subsequently adapted to an epifaunal existence, but even this cannot be proved.

The diversity of habits displayed by conical gastropods raises the important point that convergence in shell form does not guarantee similarity of function. This point is further underscored by the great difference in burrowing capacity of *Oliva*, a fast burrower, and the aptly named *Imbricaria olivaeformis* (Figure 1). Although the latter's shell shape and smooth shell exterior are closely similar to those of *Oliva* (Figure 1), the foot of *Imbricaria* is small and does not extend over the shell as it does in *Oliva*. The convergence in form between these two gastropod genera may be functionally significant (as an adaptation against shell-peeling calappid crabs, for example; see VERMEIJ, 1982), but it does not reflect convergence in locomotory function.

The burrowing gastropods that we studied broadly overlap in burrowing performance the pelecypods studied by STANLEY (1970). Some donacid and tellinid pelecypods have a higher burrowing rate index than do any of the gastropods we examined, but some south African and south Asian species of *Bullia* (Nassariidae), *Umbonium* (Umboniidae in the Trochacea), and *Oliva* are capable of extremely rapid burial and may be comparable in perfor-

mance to the fastest pelecypods (ANSELL & TREVALLION, 1969; McLACHLAN & YOUNG, 1982). Our *Oliva*, *Nassarius*, and *Natica* have burrowing performances comparable to those of many carditid, venerid, mactrid, and tellinacean pelecypods (STANLEY, 1970). Pelecypods and gastropods with a burrowing rate index ranging from 1.0 to 5.0 show morphological specializations for burrowing that are absent in the more slowly burrowing species. In pelecypods, these specializations include a large foot, a wedge-shaped anterior end, smooth or asymmetrically sculptured surface, and a flattened or cylindrical cross-sectional shape.

We conclude from our survey that most burrowing gastropods in the shallow-water sandy habitats of Guam are slow and not externally specialized for burrowing. How robust is this conclusion for the species we studied, and how applicable is it to burrowing gastropods generally? Although many of the species we studied were represented by only one individual (Table 1), our data as well as those of SIGNOR (1982a, b, 1983) indicate that the burrowing rate index varies little within species. We therefore believe that additional data, though always welcome, would not substantially alter our conclusions. The infaunal gastropod assemblage in Guam is closely similar, both taxonomically and geometrically, to other Indo-west-Pacific infaunal assemblages from shallow-water sandy environments. Assemblages from the continental shores of New Guinea, Indonesia, and the Philippines as well as those of the tropical eastern Pacific have a proportionately larger representation of potentially fast-burrowing olivids and nassariids, but probable slow burrowers such as turrids are also well represented in these faunas. It will be interesting to compare the spectrum of burrowing performances of gastropods on various continental shores with those of gastropods from more oceanic settings such as Guam.

The fact that the narrow-apertured and high-spined species that predominate in tropical Pacific infaunal gastropod assemblages burrow at all raises the question of how gastropods benefit from burrowing. A definitive answer to this question cannot be given with the presently available evidence, but active flight from predators can be safely ruled out as an important factor for all but the fastest burrowers. In Guam and elsewhere, burrowing gastropods that prey on other gastropods are by far the fastest among the infaunal gastropods, in both a relative and an absolute sense. The two species of *Oliva* that we studied were the only gastropods capable of burrowing completely in less than 1 min. All other species, including much smaller ones, feed on animals other than gastropods and required intervals of 1 min to more than 10 min to achieve complete burial, depending on the species. Gastropod-eating burrowing gastropods could, therefore, easily overtake most prey that tried to escape by burrowing. Calappid crabs, which in Guam are among the most important predators of sand-dwelling gastropods (VERMEIJ, 1982), burrow more rapidly than do any of the gastropods

we studied. Like many other infaunal crabs (SAVAZZI, 1982), calappids are able to bury themselves in 5–10 sec. We suspect that burrowing may enable infaunal gastropods and comparably slow pelecypods to remain unobtrusive to visually hunting predators such as fishes and crabs. Once they are found, these prey rely chiefly on armor for their defense (VERMEIJ, 1982). Even for species that are potentially fast enough to burrow away from enemies, escape over the surface of the sediment may be more effective. Many rapidly burrowing gastropods (some olivids, naticids, and umboniids) and pelecypods (cardiids, macrtrids, solenids) typically jump or swim away from predators before reburrowing (STANLEY, 1970). It is possible that burrowing constituted an effective method of escape when it first evolved, but evolutionary strides in the major predators of gastropods have probably made burrowing by gastropods chiefly a way of preventing detection.

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